IMPACTS OF SEA OTTER PREDATION ON COMMERCIALLY IMPORTANT SEA CUCUMBERS (*PARASTICHOPUS CALIFORNICUS*) IN SOUTHEAST ALASKA

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A

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Abstract

Consequences from management actions, particularly those regarding species reintroductions, are not always immediately apparent. After sea otters were extirpated from Southeast Alaska in the 18th and 19th century fur trade, it is presumed that marine invertebrate stocks grew in the absence of sea otter predation. Since reintroduction in the 1960s, the Southeast Alaska sea otter population has grown, with great potential to deplete the commercially important sea cucumber, *Parastichopus californicus*. This study evaluates the interaction with and impacts of sea otters on sea cucumbers using foraging observations and sea cucumber density data collected for fishery management. Sea otter diets, in terms of edible biomass, include about only 5% cucumbers, and yet sea otters are depleting sea cucumbers; declines in sea cucumber density at sea otter affected transects ranged from 26 to 100%. Sea otter predation should be included in sea cucumber fishery management, possibly as an additional form of mortality in the surplus production model, as a step toward ecosystem based management.

Table of Contents

Page

List of Figures

Page

List of Tables

Page

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General Introduction

Sea otters have a long history of over-exploitation, which has resulted in dramatic implications for ecosystems and fisheries. The southern sea otter (*Enhydra lutris nereis*) is located exclusively off California, while the northern sea otter (*Enhydra lutris*) is located along the northwest coast of the United States and Canada and the Asian coast of Russia (Kenyon 1969); both were severely reduced by fur traders in the 18th and 19th centuries. Sea otters were completely removed from Southeast Alaska by 1911 (Kenyon 1969), which had consequences to the nearshore ecosystem because sea otters act as keystone predators and must eat up to 25% of their body weight every day (Estes et al. 2003b, Oftedal et al. 2007). The classic example of a trophic cascade involves killer whales (*Orcinus orca*), humans, sea otters, sea urchins (*Strongylocentrotus* spp.), and kelp forests (Estes et al. 1989, Estes et al. 1998). In the absence of killer whale predation on otters or exploitation of otters by humans, sea otters keep sea urchin populations in check, and kelp communities can thrive. Based on sea otter biology and comparisons of prey populations in areas with and without sea otters, it is likely that without this keystone predator, many marine invertebrate stocks increased (Estes and VanBlaricom 1985). Lucrative commercial fisheries developed in Southeast Alaska in the 1980s, including those for red sea urchin (*Strongylocentrotus fransicanus*), pinto abalone (*Haliotis kamtschatkana*), Dungeness crab (*Cancer magister*), geoduck clam (*Panopea generosa*), and sea cucumber (*Parastichopus californicus*) (Pritchett and Hoyt 2008). At least some of these fisheries may not have been possible if sea otters were not hunted to extirpation (Bodkin et al. 2004).

The Alaska Department of Fish and Game (ADF&G) translocated 413 sea otters from Prince William Sound and Amchitka Island to seven locations along coastal Southeast Alaska between 1965 and 1969: Yakutat Bay, Cape Spencer, Yakobi Island, Khaz Bay, Biorka Island, Maurelle Islands and Barrier Islands (Burris and McKnight 1973). Sea otters have since expanded from those seven translocation sites and currently occupy most of the outer coast of Southeast Alaska (Figure 1). Survey efforts by the US Fish and Wildlife Service (USFWS) indicate that the population increased rapidly to 8,949 individuals by 2003 and grew at a rate of 13% per year between 2003 and 2010 (Esslinger and Bodkin 2009, V. Gill, USFWS Anchorage, AK, personal communication, 2012).

Mortality from predation and hunting may not be severe enough to reduce population growth rates of sea otters in Southeast Alaska. Killer whale predation is thought to be responsible for the declining sea otter population in the Aleutians because killer whale prey populations of Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*) are significantly depleted (Estes et al. 1998). While harbor seals have experienced a comparable decline in Glacier Bay, Steller sea lion and harbor seal populations are either stable or increasing in the Sitka and Ketchikan areas, respectively (Small et al. 2003). Alaska Natives are permitted to harvest sea otters; however, the harvest is highly regulated and punishment for non-compliance can be severe. Thus, the harvest rate has been minimal (Esslinger and Bodkin 2009), with 317 sea otters harvested

in 2011, 73 more sea otters than in 2010. Annual sea otter harvest has risen dramatically in two predominantly commercial fishing communities in Southeast Alaska, Craig and Petersburg, where harvest has increased from 15 to 192 between 2008 and 2011 (V. Gill, USFWS Anchorage, AK, personal communication, 2012).

Sea otter recolonization along the west coast of North America demonstrates rapid population growth in sea otters and major impacts on prey populations. Between 1969 and 1970, sea otters were reintroduced into Washington (Jameson et al. 1986), California (Odemar and Wilson 1969), Vancouver Island, British Columbia (Bigg and MacAskie 1978), and Attu Island, Alaska (Estes 1990). Estimates of initial population growth rates exceeded 16% per year in Washington (Jameson et al. 1986), Vancouver Island, British Columbia (Estes 1990), and Attu Island, Alaska (Estes 1990); however, population growth rates in California have remained lower at 5 to 7.8% per year, probably due to limited habitat and resources and mortality among mature females (Estes 1990, Estes et al. 2003a). The reintroduction of sea otters into Washington significantly affected invertebrates, particularly sea urchins and abalone, by reducing sea otter prey size, abundance, and distribution (Kvitek et al. 1989). For example, Kvitek et al. (1989) investigated clam selection and clam availability in sea otter foraging areas in Washington that varied in length of sea otter occupation. In long-occupied sites, average clam size available was 41 mm, which was 32 mm less than average clam size available in recently occupied sites; however, clam sizes selected by sea otters remained high, near 58 mm (Kvitek et al. 1989). Sea otters in California, Vancouver Island, and Attu Island

also negatively affected prey species densities (Morris et al. 1981, Ostfeld 1982, Estes et al. 2010) and size distributions (Hines and Pearse 1982, Kvitek et al. 1992, Estes and Duggins 1995) during recolonization. Abundance of Dungeness crabs diminished following sea otter arrival in Prince William Sound, and Dungeness crabs were virtually absent in areas of Prince William Sound occupied by sea otters for at least 30 years (Garshelis et al. 1986). Recolonizing northern sea otters experience an initial period of rapid population growth and exploit commercially valuable prey species, particularly sea urchins.

The expanding sea otter population threatens several fisheries in Southeast Alaska. Numerous sea urchin fishery management areas have experienced emergency closures due to low biomass, and the Southeast Alaska abalone fishery has been permanently closed since 1996 due to low abundance. It is unlikely that the abalone stock will recover and support a commercial fishery (Hebert and Pritchett 2002). The sea cucumber guideline harvest level (GHL) in Southeast Alaska has declined and nine fishing sub-districts have been closed due to low sea cucumber biomass; each of these sub-districts has sea otters (Rumble and Hebert 2011).

Sea otters forage over a wide range of habitat types and water depths and can modify their foraging behavior as prey resources change (Kvitek et al. 1992). Male and female otters exhibit different foraging patterns; 85% of foraging time by female sea otters occurred in shallow water (5-20 m), while male otter foraging patterns exhibited a

bimodal pattern where about 36% of foraging dives occurred in shallow water (5-20 m) and about 55% in deeper water (30-60 m) (Bodkin et al. 2004). Due to extremely high metabolic demands, sea otters must maximize foraging efficiency under competitive conditions and with declining prey resources, often achieved through specialization or diet diversification. Specialization may alleviate competition by allowing sea otters to exploit invertebrate prey more effectively through improved search and handling efficiency (Oftedal et al. 2007) and allowing individual foraging preferences to be sustained over the long term. The degree of specialization varies among populations and habitats (Tinker et al. 2007) and is less likely in food-rich sites or where sea otter density is low (e.g. San Nicolas Island, California) (Tinker et al. 2008). Additionally, as prey density decreases, the mean search time increases, which makes it less profitable to skip a prey item, even if it is of lower energetic value (Schoener 1971, Ostfeld 1982). For example, Laidre and Jameson (2006) observed foraging sea otters on the outer coast of Washington, an area of long-term occupation, and sea otters in the Strait of Juan de Fuca, a recently colonized area. Sea otters off the outer coast had diverse diets with 10 prey species or groups, containing no more than 1% sea urchins. Conversely, the newly established sea otter population at the Strait of Juan de Fuca had restricted diets consisting of 60% red sea urchins, with the remainder of the diet being predominately bivalves and purple sea urchins (*Strongylocentrotus purpuratus*) (Laidre and Jameson 2006).

The California sea cucumber (*Parastichopus californicus*), hereafter referred to as sea cucumber, is distributed from Baja California, Mexico to as far north as Kodiak Island, Alaska and occupies nearshore waters to depths exceeding 249 m (Lambert 1997, Woodby et al. 2000). It occurs in nearshore habitats that have minimal freshwater input, moderate current speeds, and are composed of mixed substrate (Woodby et al. 2000). Average sea cucumber weight in Southeast Alaska ranged from 134 to 289 g in 2010 (Hebert 2010) and lengths can exceed 50 cm. Once established in an area, sea cucumbers have little directed movement; they randomly move, on average, 2.9 to 3.9 $m \cdot day^{-1}$, although movement rates can exceed 8 $m \cdot day^{-1}$ near Juneau, Alaska (Da Silva et al. 1986, Cieciel et al. 2009). Sexual maturity is reached after about four years (Lambert 1997); they broadcast spawn annually in shallow water from June through August (Cameron and Fankboner 1986). Larvae remain planktonic for as little as 65 to 120 days, at which time metamorphosis and settlement occurs (Cameron and Fankboner 1989). Seasonal atrophy is responsible for the loss of viscera each fall and can result in a 25% loss in total sea cucumber mass; regeneration occurs in December through January (Fankboner and Cameron 1985). Predation may play an important role in sea cucumber population dynamics (Francour 1997); the sunflower star (*Pycnopodia helianthoides*) is perhaps the most widely studied of the few known predators of sea cucumbers in Alaska (Cameron and Fankboner 1989), and sea otter predation on sea cucumbers in Alaska has been observed (Watt et al. 2000).

Sea cucumbers are deposit feeders, a feeding method that acts as a form of bioturbation and plays a dominant role in manipulating sediments and altering habitat suitability for other species (Lopez and Levinton 1987). They feed on detritus by repeatedly extending tentacles from the pharynx to the substrate, collapsing them, and withdrawing them once deposited particles have adhered to their surface (Cameron and Fankboner 1984). This engineering activity allows them to subsist on a very poor food source (Lopez and Levinton 1987) while enhancing the organic matter content of the benthos by concentrating otherwise dispersed organic material in the form of fecal pellets (Sloan and Von Bodungen 1980). Fecal pellets can be regarded as high-energy spots, which contribute to particulate organic matter resuspension, enhanced substrate for settlement and growth of other species, and nutrient cycling (Sloan and Von Bodungen 1980, Conde et al. 1991). Even organisms with small individual impacts can have large cumulative ecological effects, as long as they occur at high densities over sizeable areas for sufficient periods of time (Jones et al. 1994).

The commercial fishery for sea cucumbers in Southeast Alaska began in 1981 and is managed under a complex management scheme that balances commercial and subsistence interest (Hebert and Pritchett 2002). A maximum of two quota-holding divers per vessel harvest sea cucumbers by hand by means of SCUBA or "hooka" diving, a diving method not involving SCUBA tanks, where air is supplied via an air compressor on deck. Each diver may harvest no more than 2000 lbs of sea cucumbers per trip (Hebert and Pritchett 2002). In response to increased effort in the fishery, ADF&G

developed the Southeast Alaska Sea Cucumber Commercial Fisheries Management Plan in 1990, which protects subsistence opportunities for rural Alaskans and promotes sustainable commercial harvest of sea cucumbers (Hebert and Pritchett 2002). A key component of the plan is the designation of seven areas closed to fishing (Hebert and Pritchett 2002). These management control areas are crucial for understanding population dynamics of sea cucumbers in response to fishing effort and they are currently located in areas with and without sea otter occupation. The sea cucumber fishery is managed using a surplus production model (Woodby et al. 1993) that specifies a harvest rate of no more than 18.6% every three years for sub-districts open to commercial harvesting (Clark et al. 2009). Harvest takes place on a three-year rotational cycle, where each sub-district is given two years to "rest" before it is surveyed and harvested again. The average annual harvest from 1990-2005 in Southeast Alaska is 82,936 lbs (Clark et al. 2009), and sea cucumbers had an average ex-vessel value of $\$2.52 \cdot lb^{-1}$ in 2011, the highest value in the history of the fishery (Rumble and Hebert 2011).

Even with a conservative approach to management, many areas open to harvest in Southeast Alaska have experienced a reduction in sea cucumber biomass (Hebert and Pritchett 2002). Understanding the interaction between sea otters and sea cucumbers is important to determine if, and to what degree, the declines in sea cucumber biomass observed in Southeast Alaska can be attributed to sea otters. A complex interaction of factors may influence stock biomass, but a firm understanding of the primary drivers is necessary for managing the resource.

References

Bigg, M.A., and MacAskie, I.B. 1978. Sea otters re-established in British Columbia. J. Mammal. **59**:874-876.

Bodkin, J.L., Esslinger, G.G., and Monson, D.H. 2004. Foraging depths of sea otters and implications to coastal marine communities. Mar. Mamm. Sci. **20**:305–321.

Burris, O.E., and McKnight, D.E. 1973. Game transplants in Alaska. Alaska Department of Fish and Game, Division of Game, Game Technical Bulletin 4.

Cameron, J.L., and Fankboner, P.V. 1984. Tentacle structure and feeding processes in life stages of the commercially important sea cucumber *Parastichopus californicus* (Stimpson). J. Exp. Mar. Biol. Ecol. **81**:193-209.

Cameron, J.L., and Fankboner, P.V. 1986. Reproductive biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata: Holothuroidea). I. Reproductive periodicity and spawning behavior. Can. J. Zool. **64**:168-175.

Cameron, J.L., and Fankboner, P.V. 1989. Reproductive biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata: Holothuroidea). II. Observations on the ecology of development, recruitment, and juvenile life stage. J. Exp. Mar. Biol. Ecol. **127**:43-67.

Cieciel, K., Pyper, B., and Eckert, G.L. 2009. Tag retention and the effects of tagging on movement of the giant red sea cucumber *Parastichopus californicus*. N. Am. J. Fish. Manage. **29**:288-294.

Clark, J., Pritchett, M., and Hebert, K. 2009. Status of sea cucumber stocks in southeast Alaska and evaluation of the stock assessment program. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Data Series 09-12.

Conde, J.E., Diaz, H., and Sambrano, A. 1991. Disintegration of holothurian fecal pellets in beds of the seagrass *Thalassia testudinum*. J. Coast. Res. **7**:853-862.

Da Silva, J., Cameron, J.L., and Fankboner, P.V. 1986. Movement and orientation patterns in the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Holothuroidea: Aspidochirotida). Mar. Freshwater. Behav. Physiol. **12**:133-147.

Esslinger, G.G., and Bodkin, J.L. 2009. Status and trends of sea otter populations in southeast Alaska, 1969–2003. U. S. Geological Survey, Scientific Investigations Report 2009–5045.

Estes, J.A. 1990. Growth and equilibrium in sea otter populations. J. Anim. Ecol. **59**:385-401.

Estes, J.A., and Duggins, D.O. 1995. Sea otters and kelp forests in Alaska - generality and variation in a community ecological paradigm. Ecol. Monogr. **65**:75-100.

Estes, J.A., Duggins, D.O., and Rathbun, G.B. 1989. The ecology of extinctions in kelp forest communities. Conserv. Biol. **3**:252–264.

Estes, J.A., Hatfield, B.B., Ralls, K., and Ames, J. 2003a. Causes of mortality in California sea otters during periods of population growth and decline. Mar. Mamm. Sci. **19**:198-216.

Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., and Lyon, B.E. 2003b. Individual variation in prey selection by sea otters: patterns, causes and implications. J. Anim. Ecol. **72**:144-155.

Estes, J.A., Tinker, M.T., and Bodkin, J.L. 2010. Using ecological function to develop recovery criteria for depleted species: sea otters and kelp forests in the Aleutian Archipelago. Conserv. Biol. **24**:852-860.

Estes, J.A., Tinker, M.T., Williams, T.M., and Doak, D.F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282**:473-476.

Estes, J.A., and VanBlaricom, G.R. 1985. Sea-otters and shellfisheries. *In* Marine mammals and fisheries. *Edited by* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne. Allen and Unwin, London, pp. 187-235.

Fankboner, P.V., and J.L., Cameron. 1985. Seasonal atrophy of the visceral organs in a sea cucumber. Can. J. Zool. **63**: 2888-2892.

Francour, P. 1997. Predation on holothurians: a literature review. Invertebr. Biol. **116**:52-60.

Garshelis, D.L., Garshelis, J.A., and Kimker, A.T. 1986. Sea otter time budgets and prey relationships in Alaska. J. Wildl. Manage. **50**:637-647.

Hebert, K. 2010. Southeast Alaska sea cucumber stock assessment surveys in 2010. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Data Series 10-88.

Hebert, K., and Pritchett, M. 2002. Report to the board of fisheries, miscellaneous dive fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report IJ02-45.

Hines, A.H., and Pearse, J.S. 1982. Abalones, shells, and sea otters: dynamics of prey populations in central California. Ecology **63**:1547-1560.

Jameson, R.J., Kenyon, K.W., Jefferies, S., and VanBlaricom, G.R. 1986. Status of a translocated sea otter population and its habitat in Washington. Murrelet **67**:84-87.

Jones, C.G., Lawton, J.H., and Shachak, M. 1994. Organisms as ecosystem engineers. Oikos **69**:373-386.

Kenyon, K.W. 1969. The sea otter in the eastern Pacific Ocean. Dover Publications, New York.

Kvitek, R.G., Oliver, J.S., DeGange, A.R., and Anderson, B.S. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecology **73**:413-428.

Kvitek, R.G., Shull, D., Canestro, D., Bowlby, E., and Troutman, B.L. 1989. Sea otters and benthic prey communities in Washington State. Mar. Mamm. Sci. **5**:266-280.

Laidre, K.L., and Jameson, R.J. 2006. Foraging patterns and prey selection in an increasing and expanding sea otter population. J. Mammal. **87**:799-807.

Lambert, P. 1997. Sea cucumbers of British Columbia, Southeast Alaska, and Puget Sound. University of British Columbia Press, Vancouver.

Lopez, G.R., and Levinton, J.S. 1987. Ecology of deposit feeding animals in marine sediments. Quart. Rev. Biol. **62**:235-260.

Morris R., Ellis, D.V., and Emerson, B.P. 1981. The British Columbia transplant of sea otters *Enhydra lutris*. Biol. Conserv. **20**:291-295.

Odemar, M.W., and Wilson, K.C. 1969. Results of sea otter capturing, tagging and transplanting operations by the California Department of Fish and Game. California Fish and Game, Marine Resource Operations Report 70-5.

Oftedal, O.T., Ralls, K., Tinker, M.T., Green, A. 2007. Nutritional constraints on the southern sea otter in the Monterey Bay National Marine Sanctuary. Monterey Bay National Marine Sanctuary and the Marine Mammal Commission, Washington, D.C., Technical Report.

Ostfeld, R.S. 1982. Foraging strategies and prey switching in the California sea otter. Oecologia **53**:170-178.

Pritchett, M., and Hoyt, Z. 2008. Report to the Board of Fisheries, Miscellaneous Dive Fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Management Report 08-63.

Rumble, J., and Hebert, K. 2011. Report to the Board of Fisheries, Miscellaneous Dive Fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Management Report 11-59.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. **2**:369-404.

Sloan, N.A., and Von Bodungen, B. 1980. Distribution and feeding of the sea cucumber *Isostichopus badinotus* in relation to shelter and sediment criteria of the Bermuda Platform. Mar. Ecol. Prog. Ser. **2**:257-264.

Small, R.J., Pendleton, G.W., and Pitcher, K.W. 2003. Trends in abundance of Alaska harbor seals, 1983–2001. Mar. Mamm. Sci. **19**:344–362.

Tinker, M.T., Bentall, G, and Estes, J.A. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc. Natl. Acad. Sci. USA. **105**:560-565.

Tinker, M.T., Costa, D.P., Estes, J.A., and Wieringa, N. 2007. Individual dietary specialization and dive behaviour in the California sea otter: Using archival time–depth data to detect alternative foraging strategies. Deep Sea. Res. II (Topical Stud. Oceanogr.). **54**:330–342.

Watt, J., Siniff, D.B., and Estes, J.A. 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. Oecologia **124**:289-298.

Woodby, D.A., Kruse, G.H., and Larson, R.C. 1993. A conservative application of a surplus production model to the sea cucumber fishery in southeast Alaska. Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Univ. Alaska Fairbanks, Alaska Sea Grant Program Rep. AK-SG-93-02.

Woodby, D., Smiley, S., and Larson, R. 2000. Depth and distribution of *Parastichopus californicus* near Sitka, Alaska. Alaska Fish. Res. Bull. 7:22–32.

Chapter 1: Impacts of sea otter predation on commercially important sea cucumbers (*Parastichopus californicus*) in Southeast Alaska[1]

Abstract

Sea cucumbers (*Parastichopus californicus*), which are an important commercial, subsistence and ecological resource, are negatively impacted by an expanding sea otter (*Enhydra lutris*) population in Southeast Alaska. Sea otters were reintroduced into Southeast Alaska in the 1960s after their demise in the 18th and 19th century fur trade; in the ensuing decades, the otter population grew, and sea cucumber biomass declined. This study evaluates the interaction and effects of sea otters on sea cucumbers using sea cucumber foraging observations and survey data and sea cucumber density data collected for fishery management. Sea cucumbers represented about 5% of the sea otter diet in biomass. Declines in sea cucumber density ranged from 26 to 100% in areas with sea otters and were greatest within areas with high sea otter use. Sea cucumber density was lower in areas sea otters inhabited longer. Sea otter predation should be included in sea cucumber fishery management, possibly as an additional form of mortality in the surplus production model used to set annual GHLs, as a step toward ecosystem based management.

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Introduction

The reestablishment of sea otters (*Enhydra lutris*) in Southeast Alaska to areas where they were absent for nearly a century has created a conflict with the California sea cucumber (*Parastichopus californicus*) fishery and subsistence resource users. Sea otters were hunted to near extinction during the 18th and 19th century fur trade and were extirpated from Southeast Alaska by 1911 (Kenyon 1969). In the ensuing decades, sea cucumber population abundance likely increased in the absence of sea otter predation, and a lucrative commercial dive fishery began in 1981 (Rumble and Hebert 2011). The Southeast Alaska sea cucumber fishery includes 289 active permit holders; 180 of those reported landings during the 2010-2011 season for an ex-vessel value exceeding $3,200,000 (Rumble and Hebert 2011). Between 1996 and 2011 a loss of over $5,000,000 in ex-vessel revenue was estimated due to sea otter predation (McDowell Group 2011). This loss represents the annual unaccounted loss of biomass, biomass exceeding that removed by the fishery, and the associated ex-vessel price for a given year. Sea otter predation in Southeast Alaska is suspected to have resulted in the closure of nine sea cucumber fishery sub-districts and a decline in sea cucumber density in others, resulting in a reduction in guideline harvest level for the commercial fishery (Rumble and Herbert 2011). Surprisingly few data exist addressing the impacts of sea otter predation on its prey in Southeast Alaska or the relative value of sea cucumbers in the sea otter diet. Sea otters are expanding into recently unoccupied and historically occupied habitats, which provides an opportunity to test the effects of sea otter predation on sea cucumbers. Fishing can depress sea cucumber stocks (Schroeter et al. 2001, Friedman et al. 2011),

and this study attempts to separate declines in sea cucumber density resulting from sea otter predation from those resulting from commercial fishing.

The Alaska Department of Fish and Game (ADF&G) translocated 413 sea otters from Prince William Sound and Amchitka Island to coastal Southeast Alaska between 1965 and 1969 (Burris and McKnight 1973). Sea otters currently occupy most of coastal Southeast Alaska and their range expansion was documented in 1988 (Pitcher 1989), 1994 (Agler et al. 1995), 1997 (Hodges et al. 2008), 2003 (Esslinger and Bodkin 2009), and 2010 (V. Gill, USFWS Anchorage, AK, personal communication, 2012) (Figure 1). The population in southern Southeast Alaska grew at a rate of 13% per year between 2003 and 2010 (V. Gill, USFWS Anchorage, AK, personal communication, 2012).

Due to high metabolic demands and limited capacity to store energy, sea otters must consume up to 25% of their body weight per day (Estes et al. 2003, Oftedal et al. 2007). Consequently, the abundance and size distribution of their prey can be significantly reduced (Kvitek et al. 1989, Kvitek et al. 1992, Estes and Duggins 1995). A trophic cascade in Southeast Alaska involves humans, sea otters, sea urchins, and kelp forests (Estes and Duggins 1995). In the absence of exploitation by humans, and in the presence of sea otters, sea urchin populations are kept in check and kelp communities can thrive. Diet diversification has been observed for northern sea otters in Washington (Laidre and Jameson 2006) and southern sea otters in California (Ostfeld 1982, Tinker et al. 2008), where the depletion of preferred prey resulted in greater consumption of less desirable

prey. Sea cucumbers have a very low energy content of 1744 cal·g^{-1}, compared to 3905 cal·g^{-1} for a butter clam and 4249 cal·g^{-1} for a geoduck (Oftedal et al. 2007), and as a result may be less desirable to sea otters as prey.

The objective of this study is to investigate the interaction between sea otters and sea cucumbers to determine the extent which sea otters are negatively affecting sea cucumbers in Southeast Alaska. Here, we use foraging observations, kernel density estimation (KDE), and a Before-After, Control-Impact (BACI) approach to examine (1) how sea otter diet and handling time vary with time since colonization, and (2) changes in sea cucumber density in the presence and absence of sea otters.

Methods

Study Area

Foraging observations were taken from various locations in Southeast Alaska in June through August of 2010 and 2011 (Figure 1). Locations were representative of the region and varied in habitat type and time since sea otter colonization, i.e., persistence. Areas of longest, long, intermediate, and recent sea otter persistence had sea otters by 1988 (Pitcher 1989), 1994/1997 (Agler et al. 1995, Hodges et al. 2008), 2003 (Esslinger and Bodkin 2009), and 2010 (V. Gill, USFWS Anchorage, AK, personal communication, 2012), respectively (Figure 1). Data were collected from south to north, Barrier Islands and adjacent Prince of Wales shoreline, SW Dall Island, NW Dall Island, Maurelle

Islands, Lulu Island and immediate surrounding area, Totem Bay and immediate surrounding area, Tebenkof Bay, and NW Kupreanoff Island (Table 1).

Observations of Foraging Sea Otters

Field observations of foraging sea otters were used to create several indices of predation on sea cucumbers. Methods were adapted from Kvitek et al. (1993), where Questar telescopes and binoculars were used to make observations on individual foraging otters from shore. Researchers observed an individual sea otter until it had either stopped foraging, 20 foraging dives had been observed, or it was lost from view. The date, location, sex, and the presence of a pup were noted for each otter observed. The dive time, surface interval, prey type, number of prey, and prey size were recorded for each foraging dive observed. Prey were identified to species, or next nearest taxonomic group, and prey size was estimated by comparing the prey item to sea otter paw width, or multiple thereof (VanBlaricom 1988); some prey were unidentified and were labeled as such. Prey size in relative sea otter paw width was transformed to prey diameter (mm) (United States Geological Service, Alaska Science Center, Anchorage, AK, unpublished data), and transformed to total edible biomass using estimates of prey biomass at size from Glacier Bay, Alaska (United States Geological Service, Alaska Science Center, Anchorage, AK, unpublished data). Edible biomass for sea cucumbers was found using an exponential length-weight regression formula (Cone 1989), biomass=1.14*diameter $^{1.83}$, using length and biomass data from sea cucumber samples randomly collected by ADF&G during 2007 dive surveys (Zac Hoyt, ADF&G, Petersburg, AK, unpublished

data). The biomass of unidentified species was determined by size specific mean values obtained for all identified species. Sea cucumber handling time was defined as the total time from the time an otter surfaced until it finished eating the prey item. Foraging data were grouped into "sites", with the criteria that data within a site had the same level of sea otter persistence and data within a site were separated by no more than 8 km (Figure 1).

Tests of the Sea Otter Diet

Differences in percent diet, in edible biomass weight, consisting of sea cucumbers, handling times, and relative sea cucumber consumption by males vs. females, i.e., the number of sea cucumbers eaten by male sea otters divided by the number of sea cucumbers eaten by male and female sea otters, were examined at each sea otter persistence category. Response values were arcsine transformed to meet conditions of normality and differences were examined using analysis of variance (ANOVA; generalized linear model), with sea otter persistence as the categorical predictor variable. If ANOVA results were significant, differences among factor levels were assessed with Tukey's Honestly Significant Difference (Tukey HSD).

Sea Cucumber Density

ADF&G research divers surveyed sea cucumbers annually in Southeast Alaska to assess sea cucumber abundance for fishery management, and up to 500 strip transects were sampled each year (Hebert 2010). A pair of two meter wide transects ran perpendicular

to the shore and extended from the water's edge to 15 m below mean lower low water. Transect length varied depending slope of the bottom. The location for the first transect pair in a sub-district was randomly chosen, while subsequent transect pairs were distributed equally along the shoreline; distances between transect pairs equaled total shoreline length divided by the number of transect pairs. Areas usually contained 15 – 25 transect pairs, depending on variety of habitat quality and sub-district size. Fishery sub-districts, hereafter fished areas, and management control sub-districts, hereafter unfished areas, were surveyed once every three years and every year, respectively (Figure 1, Hebert 2010). Primary substrate type (rock, gravel, shell, sand, boulder, mud, silt, woody, or cobble), number of sea cucumbers per transect, and average sea cucumber weight were recorded with each survey. Estimates of total number of sea cucumbers in a sub-district were generated by multiplying the length of linear shoreline in a sub-district by the average number of cucumbers per m shoreline to 15 m depth in the transects. Total number of sea cucumbers from a transect pair was divided by total length of shoreline the transects encompassed (4 m) to get an average number of sea cucumbers per linear m shoreline to 15 m depth, hereafter density, to be used for comparison in our study. Sea cucumber density was calculated using data from 1990 to 2011 from transects south of 57°35'00"N.

Tests of the Effects of Sea Otters

Differences in sea cucumber density before and after sea otter colonization at control transects without sea otters and impact transects with sea otters were examined using a

Before-After, Control-Impact (BACI) design (Smith 2002) with two-way ANOVA and interactions; significance in the interaction implies that sea otters are having an effect (Green 1979). Primary substrate type and a unique transect identifier (to account for spatial correlation) were included in the model. Separate analyses were performed at three different levels of sea otter persistence, i.e., length of occupancy. Surveys were discontinued at some transects and new transects were added to the survey; thus, only transects with survey data before and after sea otter arrival and within fished areas were included. Before and after periods for areas with long sea otter persistence were 1990-1992 and 2009-2011, respectively. Before and after periods for areas with intermediate sea otter persistence were 1994-1996 and 2009-2011, respectively. Before and after periods for areas with recent sea otter persistence were 2004-2005 and 2010-2011, respectively. An underlying assumption of the BACI analyses is that the data are additive (Stewart-Oaten et al. 1986); additivity was achieved with a log transformation. Differences in mean sea cucumber density across levels of sea otter persistence were compared with ANOVA and Tukey HSD.

Sea otter ranges in 2003 and 2010 were calculated using sea otter distribution and abundance surveys (Esslinger and Bodkin 2009, V. Gill, USFWS Anchorage, AK, personal communication, 2012), and kernel density estimation (Worton 1989). Kernel density estimation was used to create probability density functions for sea otter counts in 2003 and 2010 and then isopleth lines were used to delineate total ranges and core areas, i.e., areas containing 95% and 50% of the probability density functions, respectively.

Kernel density estimation was performed with a Gaussian kernel (Sheather 2004), a grid resolution of 100 m, and a bandwidth estimated using the least squares cross-validation algorithm (Worton 1989). Sea otter ranges for 2003 and 2010 were combined into three sea otter use categories; areas of high use were in core areas during both 2003 and 2010 sea otter surveys, areas of moderate use were in core areas during one survey, and areas with low use were in the total range during one or both surveys (Figure 2). To examine differences in sea cucumber density before and after sea otter colonization in areas with high, moderate, and low use by sea otters, a two-way ANOVA with an interaction between sea otter use category and before or after periods was used. A linear model was used to test correlation between the combined kernel density estimates, i.e., the combined values of the probability density functions for sea otter counts in 2003 and 2010, and sea cucumber density from 2009 to 2011.

Tests of the Effects of Fishing

To identify the effect of fishing on sea cucumbers, changes in sea cucumber density through time and overall sea cucumber density in unfished areas were compared with changes and overall density in their neighboring fished areas using two-way repeated measures ANOVA. Separate analysis were performed for each unfished area and their neighboring fished areas; i.e., areas within 10 km of an unfished area. There were four unfished areas in the study area; sea otters impact areas 103-40 and 103-60, while sea otters do not impact areas 101-27 and 106-30. Five, three, four, and two fished areas were considering neighboring fished areas to unfished areas 103-40, 103-60, 101-27, and

106-30, respectively. Unfished areas 103-40 and 103-60 are located along the west coast of Prince of Wales Island near Hydaburg and Craig, respectively, 106-30 is located on the northeast coast of Prince of Wales Island, and 101-27 is located along the south coast of Gravina Island, near Ketchikan. Model factors included area type (fished or unfished), survey year of sea cucumber density estimates, and their interaction, with individual transect ID as the error term. Significance in the interaction implies that the trend in sea cucumber density through time differs between unfished and fished areas.

RStudio version 0.94.110 was used for all statistical analyses and figures; ArcGIS 10 was used to manipulate, code data, and to create maps; and Geospatial Modeling Environment (Spatial Ecology LLC) was used for kernel density estimation. All statistical tests were performed with a statistical significance of $p=0.05$.

Results

Observations of Foraging Sea Otters

Foraging observations were recorded for 336 sea otters and 3,404 successful foraging dives. Sea otters consumed 58 sea cucumbers; the minimum and maximum sea cucumber consumed had a calculated edible biomass of 14 g and 332 g, respectively, with a mean ± SD size of 147 ± 60 g. Mean ± SD percent of the diet, by edible biomass weight, consisting of sea cucumbers was 5 ± 8% at all sites and 13 ± 8% for sites where sea cucumbers were observed in the sea otter diet. Sea otters foraged on 58 prey species and the remainder of the sea otter diet consisted primarily of red sea urchins, clams,

including geoducks (*Panopea generosa*), and crabs; about 2% of the sea otter diet, in weight, was from unidentified prey. Mean ± SD handling time was 125 ± 59 s, and relative sea cucumber consumption by males vs. females was 47 ± 38%. The percent diet consisting of sea cucumbers, handling times, and relative sea cucumber consumption by males vs. females did not differ significantly among sea otter persistence categories (Table 2, Figure 3).

Sea Cucumber Density

Sea otters negatively impact sea cucumber density in Southeast Alaska (Table 3, Figure 4). Sea cucumber density decreased 100.0% after being impacted by otters in 1994, compared to a 19.6% decline at control transects (Figure 4a). Sea cucumber density decreased 80.1% after being impacted by sea otters in 2003, compared to an 19.1% decline at control transects (Figure 4b). Sea cucumber density decreased 25.8% after being impacted by sea otters in 2010, while sea cucumber density at control transects decreased 15.4% over this time period (Figure 4c).

Sea cucumber density was significantly lower where sea otters have been for longer times (Table 2, Figure 5a), with the lowest density occurring where sea otters have been since 1988; i.e., areas with longest persistence. Density in areas with longest persistence (mean ± SD, 0.1 ± 0.4) was significantly ($p<0.001$) lower than in areas with recent persistence (10.6 ± 16.6) and in areas with intermediate persistence (6.6 ± 7.5) (Figure 5a). Density in areas with long persistence was significantly ($p<0.001$) lower than in areas with recent

and intermediate persistence. Density was significantly ($p<0.001$) lower in areas with intermediate persistence than in areas with recent persistence (Figure 5a). Sea cucumber density in areas with longest sea otter persistence was not significantly different from areas with long persistence (3.9 ± 6.0) ($p=0.941$; Figure 5a).

Declines in sea cucumber density after sea otter occupation were greater in areas with higher sea otter use as determined by kernel density estimation (Table 4; Figure 5b). Sea cucumber density declined significantly 44.3, 88.1, and 99.8% in low, moderate, and high use areas, respectively (Figure 5b). Sea cucumber density decreased as sea otter kernel density estimates for 2003 and 2010 increased (Figure 6); however, the strength of the linear relationship is weak ($r^2=0.23$; $F=17.50$; $df=419$; $p<0.001$; Figure 6).

Sea cucumber density declined in all unfished and neighboring fished areas; however, trends in sea cucumber density through time were similar between unfished and fished areas, except at unfished area 103-40, where declines in sea cucumber density were significantly lower than at its neighboring fished areas (Table 5). Overall mean sea cucumber density was significantly lower at unfished area 103-60 than at its neighboring unfished areas (Table 5; Figure 5c).

Discussion

Sea otters are affecting sea cucumbers in Southeast Alaska, the extent of which depends on the duration and magnitude of sea otter presence. While sea cucumber density

declined at transects with and without sea otters, declines in areas where sea otters have existed since at least 1994, 2003, and 2010 were five, four, and two times, respectively, greater than those at the control transects without sea otters. Areas in our study within core sea otter ranges since at least 2003 were the most impacted by sea otters and have sea cucumber densities near zero. Sea cucumbers were observed in the sea otter diet in areas where sea otters have existed since at least 1994 - areas which have experienced 100% declines in sea cucumber density. This indicates that sea otters are able to find and eat sea cucumbers, even when they are at very low density. It is possible that sea cucumbers have a depth refuge and therefore are not driven locally extinct by sea otters. Sea otters generally forage in water shallower than 30 m (Bodkin et al. 2004) but sea cucumbers can be found at depths exceeding 249 m (Lambert 1997). The relatively weak effect of sea otters on sea cucumbers in recently occupied areas (2010) suggests that the effects of sea otters on sea cucumber populations are delayed, accumulate over time, and may require multiple years of survey data to detect. Other studies have observed declines in sea cucumbers. Clark et al. (2009) showed that between 1990 and 2005, 63% of areas in Southeast Alaska with at least two years of commercial harvest had significant decreases in sea cucumber density; however, they did not use sea otter abundance and distribution data to identify the relationship between sea otters and decreases in sea cucumber density.

In other studies of sea otter impacts, Dungeness crab in Orca Inlet, Prince William Sound experienced 20% declines in abundance during the first two years of sea otter occupation

from 1978 to 1980, and when large numbers of sea otters moved into the area in late 1980, crab abundance dropped by 85% in less than a year (Garshelis et al. 1986). Sea otters in Nelson Bay, Prince William Sound reduced Dungeness crab abundance by 61% between 1978 and 1979, during the first year of sea otter occupation (Garshelis et al. 1986). By 1980, five of six study sites in Prince William Sound showed reductions in Dungeness crab abundance ranging from 63-93% (Garshelis et al. 1986). Sea urchins experience dramatic and immediate impacts from sea otters; sea otters reduced sea urchin biomass by 71% in the year following their reintroduction in Washington (Laidre and Jameson 2006). Another species of sea cucumber, *Cucumaria miniata,* along the outer coast of Washington, had significantly lower densities within the primary sea otter range than in the secondary range at one of two survey sites (Kvitek et al. 1989).

Fishing could contribute to the decline in sea cucumber density in Southeast Alaska; however, declines in fished areas were not significantly different from unfished areas, which could result from a variety of factors. One possibility is that the observed declines are within the natural range of variation for this species. Clark et al. (2009) found decreases in sea cucumber density in unfished areas averaged 5.8% per year, compared to an average of 5.0% per year in fished areas, and suggested that sea cucumbers in Southeast Alaska appear to be equally affected by natural events and commercial fishing. Declines in sea cucumber density may be similar in areas open and closed to fishing because sea cucumbers have very long larval planktonic stages, up to 120 days (Cameron and Fankboner 1989), and populations are interconnected through this larval stage.

Therefore, the net decline of sea cucumbers throughout Southeast Alaska may lead to reduced larval supply and recruitment at all sites. Another possibility is that areas closed to commercial fishing are open to subsistence fishing and in close proximity to communities on Prince of Wales Island, which have a long history of sea cucumber subsistence use by Alaska Natives (Mathews et al. 1990). In 1997/1998, an estimated 19,840 lbs of sea cucumbers were collected for subsistence from 10 communities on Prince of Wales Island (Alaska Department of Fish and Game, Division of Subsistence, Juneau, AK, unpublished data, 2012). Although detailed information on subsistence use is not available, subsistence harvest is likely from areas closed to commercial fishing and may contribute to declines in sea cucumber density in these areas. When the sea cucumber fishery management plan was established, one of the intents of the creation of areas closed to commercial fishing was to provide access for subsistence users to sea cucumber resources (Gordon Kruse, University of Alaska Fairbanks, personal communication, 2012).

Fishing mortality was responsible for 33-83% of stock declines for the congener, *Parastichopus parvimensis,* in the Channel Islands, California from 1993 to 1999; however, unlike the fishery in Southeast Alaska, the *P. parvimensis* fishery in California was largely unregulated with no restrictions on size, season, or amount of harvest (Schroeter et al. 2001). Fishery quotas in Southeast Alaska are calculated from the lower bound of the 90% confidence interval of the sea cucumber biomass estimate, changes in sea cucumber biomass are estimated annually prior to harvest on a three-year rotational

basis, and areas with low biomass are not opened to fishing (Clark et al. 2009). The Southeast Alaska sea cucumber fishery is managed using a surplus production model (Woodby et al. 1993) that specifies a harvest rate of no more than 18.6% every three years for sub-districts open to commercial harvesting (Clark et al. 2009). Given the presumably conservative approach to sea cucumber management in Southeast Alaska, recruitment into the fishery may offset reductions in biomass from fishing. Sea cucumber stocks worldwide, particularly in the Indo-Pacific, have a high incidence of overexploitation; 20% of fisheries are depleted and 38% are over-exploited (Purcell et al. in press). The sea cucumber fishery in Alaska was moderately exploited between 2004 and 2008; i.e., the exploitation rate was sustainable with some potential to increase yield without diminishing the reproductive capacity of the stock. Given the high incidence of over-exploitation, radical changes to sea cucumber management worldwide are needed so that exploitation rates are sustainable (Purcell et al. in press).

Sea cucumbers represented roughly the same percentage of the sea otter diet at all levels of sea otter persistence and, when only considering sites where sea cucumbers were observed in the diet, they represented a relatively high proportion (13%) of the diet. This result is surprising, considering that sea cucumbers contain only 1744 $cal \cdot g^{-1}$, compared to 3905 $cal \cdot g^{-1}$ for a butter clam (Oftedal et al. 2007). Sea cucumbers may be preferred because they require no energetically costly excavation effort, are often found on accessible shallow-water habitats, are void of any hard calcareous protection, and do not have any potentially harmful defense mechanisms such as claws or spines. *Cucumaria*

miniata represented less than 0.1% of the sea otter diet along the outer coast of Washington and in the Strait of Juan de Fuca between 1993 and 1999 (Laidre and Jameson 2006). The low incidence of *C. miniata* in the sea otter diet may be because, unlike *P. californicus*, they are often found wedged between rocks (Lambert 1997) and may be difficult to extract, or alternatively, they may be less abundant than *P. californicus* in Southeast Alaska. Sea otters in our study selected a wide size range of sea cucumbers with a small mean ± SD size of 146 ± 60 g in relation to ADF&G estimates of mean size ranging from 134 g to 289 g (Hebert 2010); thus, sea otters likely select sea cucumbers opportunistically. Sea cucumbers have been observed in the sea otter diet at Amchitka Island, Alaska (Watt et al. 2000), Glacier Bay, Alaska (Bodkin et al. 2006), and Washington (Laidre and Jameson 2006).

Ecosystem-based management (EBM) and adaptive governance consider the biological, physical, and socio-economic components of an ecosystem (Kappel and Martone 2006) while encouraging collaboration among scientists, communities, and government agencies, and other stakeholders (Hughes et al. 2007) and could help manage uncertainty and change in the sea cucumber fishery. The long-term sustainability of sea cucumbers in Southeast Alaska and sea otters are not necessarily mutually exclusive; however, they are managed by different agencies with little interaction. These entities could share knowledge concerning sea otters and fisheries to develop a capacity to predict, prepare for, and address changes to resources and fisheries. Managers could integrate sea otters into management and evaluate and predict effects on commercially important species by

using existing dive survey data. Predation could be incorporated into the surplus production model for sea cucumbers to account for removals by sea otters. Failing to account for predation mortality in surplus production models can lead to underestimates of stock biomass and overestimates of fishery surplus production (Moustahfid et al. 2009). Information on sea otter distribution and abundance could offer a fine scale understanding of predator impacts and valuable information for fishery managers to predict areas most at risk from sea otter predation. Low sea cucumber densities result in reduced reproductive success (Purcell et al. in press); therefore, areas with sea otters may need to have more conservative sea cucumber density thresholds for fishery closures to protect spawning stock biomass. The combination of fishing and sea otter predation may drive sea cucumber to low densities, below a threshold for successful reproduction, which could prevent sea cucumber recovery even after closing fishing. The pinto abalone fishery in Southeast Alaska was closed in 1995 because of low stock biomass, yet abalone biomass continues to decline in areas with sea otters (Rumble and Hebert 2011).

This study has assumptions that address variation in sea cucumber data collection and spatial and temporal differences between impacted and control transects. First, although ADF&G sampling methods are similar across all transects, research divers with varying degrees of sampling precision often sample sea cucumbers and we assume differences in sampling is inconsequential. Second, we assumed a dynamic equilibrium, i.e., we recognize that impact and control transects have spatial and temporal variation and we

assume that natural changes in mean sea cucumber density through time at impact transects will mimic changes at control transects, and vice versa.

One of greatest challenges of adaptive management is being able to predict environmental, social, and economic change (Hughes et al. 2007). Our study demonstrates how the sea cucumber resource changes over time due to sea otter predation. Sea cucumber densities in areas without sea otters will likely decrease if and when sea otters colonize, therefore, more fishery closures should be expected if the sea otter population continues to expand. Management could be improved with knowledge of this species interaction and efforts to balance economic, socio-cultural, and environmental values and priorities; large-scale removal of sea otters is impractical and focusing only on the ecological side as a basis for management decisions is equally undesirable (Folke et al. 2005). This may require adjusting fishery thresholds and including sea otter predation as a form of natural mortality in the surplus production model for sea cucumbers. To make appropriate management decisions, agencies and stakeholders could work together to develop multiple potential management strategies, evaluate the benefits and risks associated with each, and develop performance metrics to ensure goals are met (Kappel and Martone 2006).

References

Agler, B.A., Kendall, S.J., Seiser, P.E., and Lindell, J.R. 1995. Estimates of marine bird and sea otter abundance in Southeast Alaska during summer 1994. U.S. Fish and Wildlife Service, Migratory Bird Management.

Bodkin, J.L., Ballachey, B.E., Kloecker, K.A., Esslinger, G.G., Monson, D.H., Coletti, H.A., and Estes, J.A. 2006. Sea otter studies in Glacier Bay National Park and Preserve: draft annual report 2004. Draft Annual Report. U.S. Geological Survey.

Bodkin, J.L., Esslinger, G.G., and Monson, D.H. 2004. Foraging depths of sea otters and implications to coastal marine communities. Mar. Mamm. Sci. **20**:305–321.

Burris, O.E., and McKnight, D.E. 1973. Game transplants in Alaska. Alaska Department of Fish and Game, Division of Game, Game Technical Bulletin 4.

Cameron, J.L., and Fankboner, P.V. 1989. Reproductive biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata: Holothuroidea). II. Observations on the ecology of development, recruitment, and juvenile life stage. J. Exp. Mar. Biol. Ecol. **127**:43-67.

Clark, J., Pritchett, M., and Hebert, K. 2009. Status of sea cucumber stocks in southeast Alaska and evaluation of the stock assessment program. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Data Series 09-12.

Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. **118**:510-514.

Esslinger, G.G., and Bodkin, J.L. 2009. Status and trends of sea otter populations in southeast Alaska, 1969–2003. U.S. Geological Survey, Scientific Investigations Report 2009–5045.

Estes, J.A., and Duggins, D.O. 1995. Sea otters and kelp forests in Alaska - generality and variation in a community ecological paradigm. Ecol. Monogr. **65**:75-100.

Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., and Lyon, B.E. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. J. Anim. Ecol. **72**:144-155.

Folke, C., Hahn, T., Olsson, P., and Norberg, J. 2005. Adaptive governance of social-ecological systems. Annu. Rev. Environ. Resour. **30**:441-473.

Friedman, K., Eriksson, H., Tardy, E., and Pakoa, K. 2011. Management of sea cucumber stocks: patterns of vulnerability and recovery of sea cucumber stocks impacted by fishing. Fish Fish. **12**: 75-93.

Garshelis, D.L., Garshelis, J.A., and Kimker, A.T. 1986. Sea otter time budgets and prey relationships in Alaska. J. Wildl. Manage. **50**:637-647.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York.

Hebert, K. 2010. Southeast Alaska sea cucumber stock assessment surveys in 2010. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Data Series 10-88.

Hodges, J.I., Groves, D.J., and Conant, B.P. 2008. Distribution and abundance of waterbirds near shore in southeast Alaska, 1997-2002. Northwest. Nat. **89**:85-96.

Hughes, T.P., Gunderson, L.H., Folke, C., Baird, A.H., Bellwood, D., Berkes, F., Crona, B., Helfgott, A., Leslie, H., Norberg, J., Nystrom, M., Olsson, P., Osterblom, H., Scheffer, M., Schuttenberg, H., Steneck, R.S., Tengoe, M., M., Troll, Walker, B., Wilson, J., and Worm, B. 2007. Adaptive management of the great barrier reef and the Grand Canyon world heritage areas. Ambio. **36**:586-592.

Kappel, C.V., and Martone, R.G. 2006. Ecosystem-based management. *In*: Encyclopedia of Earth. *Edited by* C.J. Clevend. Environmental Information Coalition, National Council for Science and the Environment, Washington, D.C. pp. 1-4.

Kenyon, K.W. 1969. The sea otter in the eastern Pacific Ocean. Dover Publications, New York.

Kvitek, R.G., Bowlby, C.E., and Staedler, M. 1993. Diet and foraging behavior of sea otters in southeast Alaska. Mar. Mamm. Sci. **9**:168-181.

Kvitek, R.G., Oliver, J.S., DeGange, A.R., and Anderson, B.S. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecology. **73**:413-428.

Kvitek, R.G., Shull, D., Canestro, D., Bowlby, E., and Troutman, B.L. 1989. Sea otters and benthic prey communities in Washington State. Mar. Mamm. Sci. **5**:266-280.

Laidre, K.L., and Jameson, R.J. 2006. Foraging patterns and prey selection in an increasing and expanding sea otter population. J. Mammal. **87**:799-807.

Lambert, P. 1997. Sea cucumbers of British Columbia, Southeast Alaska, and Puget Sound. University of British Columbia Press, Vancouver.

Mathews V., Kookesh, M., and Bosworth, R. 1990. Subsistence harvest and use of sea cucumber in southeast Alaska. Alaska Department of Fish and Game, Division of Subsistence, Technical Paper 190.

McDowell Group. 2011. Sea otter impacts on commercial fisheries in southeast Alaska. Prepared for: Southeast Alaska Regional Dive Fisheries Association. Juneau, Alaska.

Moustahfid, H., Tyrell, M.C., Link, J.S. 2009. Accounting explicitly for predation mortality in surplus production models: an application to longfin inshore squid. N. Am. J. Fish. Manage. **29**:1555-1566.

Oftedal, O.T., Ralls, K., Tinker, M.T., Green, A. 2007. Nutritional constraints on the southern sea otter in the Monterey Bay National Marine Sanctuary. Technical Report to the Monterey Bay National Marine Sanctuary and Marine Mammal Commission.

Ostfeld, R.S. 1982. Foraging strategies and prey switching in the California sea otter. Oecologia **53**:170-178.

Pitcher, K.W. 1989. Studies of Southeastern Alaska sea otter populations-Distribution, abundance, structure, range expansion, and potential conflicts with shellfisheries. U.S. Fish and Wildlife Service Cooperative Agreement. Final Report Part 1. Alaska Department of Fish and Game. No. 14-16-0009-954.

Purcell, S.W., Mercier, A., Conand, C., Hamel, J., Toral-Granda, M.V., Lovatelli, A., and Uthicke, S. in press. Sea cucumber fisheries: global analysis of stocks, management measures and drivers of overfishing. Fish Fish.

Rumble, J., and Hebert, K. 2011. Report to the Board of Fisheries, Miscellaneous Dive Fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Management Report 11-59.

Schroeter, S.C., Reed, D.C., Kushner, D.J., Estes, J.A., and Ono, D.S. 2001. The use of marine reserves in evaluating the dive fishery for the warty sea cucumber (*Parastichopus parvimensis*) in California, U.S.A. Can. J. Fish. Aquat. Sci. **58**:1773-1781.

Sheather, S.J. 2004. Density estimation. Stat. Sci. **19**:588-597.

Smith, E.P. 2002. BACI design. *In* Encyclopedia of Environmetrics. *Edited by* A.H. El-Shaarawi and W.W. Piegorsch. Wiley, Chichester, United Kingdom. pp. 141-148.

Stewart-Oaten A., Murdoch, W.W., and Parker, K.R. 1986. Environmental impact assessment: ''pseudoreplication'' in time? Ecology **67**:929-940.

Tinker, M.T., Bentall, G, and Estes, J.A. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc. Natl. Acad. Sci. USA. **105**:560-565.

VanBlaricom, G.R. 1988. Effects of foraging by sea otters on mussel-dominated intertidal communities. *In* The community ecology of sea otters. *Edited by* J.A. Estes. Springer-Verlag, Berlin. pp. 408-491.

Watt, J., Siniff, D.B., and Estes, J.A. 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. Oecologia **124**:289-298.

Woodby, D.A., Kruse, G.H., and Larson, R.C. 1993. A conservative application of a surplus production model to the sea cucumber fishery in southeast Alaska.

Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Univ. Alaska Fairbanks, Alaska Sea Grant Program Rep. AK-SG-93-02.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70**:164-168.

Tables

Table 1. General location and GPS coordinates of sea otter foraging observation data.

General Location	GPS Coordinates
Barrier Islands	54° 46' 26"N, 132° 24' 00"W
Hessa Inlet to	54° 46' 40"N, 132° 16' 51"W to
Hunters Bay	54° 53' 05"N, 132° 21' 10"W
Cape Muzon to	54° 40' 55"N, 132° 41' 09"W to
Dakoo Harbor	54° 42' 39"N, 132° 41' 02"W
Sea Otter Harbor to	55° 06' 07"N, 133° 14' 16"W to
Divers Bay	55° 10' 01"N, 133° 14' 31"W
Maurelle Islands	55° 36' 25"N, 133° 42' 46"W
Lulu Island	55° 31' 22"N, 133° 32' 02"W
Totem Bay	56° 27' 28"N, 133° 24' 53"W
Portillo Channel to	55° 28' 30"N, 133° 24' 14"W to
Rowan Bay	56° 39' 18"N, 134° 15' 35"W
Gill Harbor	56° 49' 51"N, 133° 58' 04"W
Security Bay	56° 49' 58"N, 134° 19' 37"W
Saginaw Bay	56° 52' 01"N, 134° 09' 18"W
Kake, Alaska Area	56° 56' 49"N, 134° 03' 03"W

Table 2. ANOVAs comparing percent sea otter diet consisting of sea cucumbers, sea cucumber handling time (s), relative sea cucumber consumption by males vs. females (%), and mean sea cucumber density (sea cucumbers per m shoreline) among sea otter persistence (longest, long, intermediate, and recent). P values, F statistics, degrees of freedom (DF), and mean squares (MS) are reported. Significance levels are indicated with an (*), where * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

Response	Source of Variation	*DF*	*MS*	*F*	*p*
Percent Diet Sea	Persistence	3	0.01	2.24	0.115
Cucumbers	Residuals	20	0.01		
Handling Time	Persistence	3	2614.61	0.90	0.503
	Residuals	5	2903.51		
Relative Consumption	Persistence	3	0.41	1.16	0.428
by Males vs. Females	Residuals	4	0.36		
Sea Cucumber Density	Persistence	3	68.63	215.42	< 0.001***
	Residuals	843	0.32		

Table 3. Before-After, Control-Impact ANOVAs comparing sea cucumber density among periods (years before sea otter impact, years after sea otter impact), impacts (areas with sea otters, areas without sea otters), and their interaction. Analyses were performed for areas with a confirmed sea otter occupation in 1994, 2003, and 2010. P values, F statistics, degrees of freedom (DF), and mean squares (MS) are reported. Significance levels are indicated with an (*), where * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

Year of Sea Otter Impact	Source of Variation	*DF*	*MS*	*F*	*p*
1994	Period	1	11.29	23.28	< 0.001***
	Impact	1	52.03	107.32	< 0.001***
	Period*Impact	1	19.78	40.80	< 0.001***
	Residuals	197	0.49		
2003	Period	1	17.92	43.35	< 0.001***
	Impact	1	79.71	192.78	< 0.001***
	Period*Impact	1	31.52	76.24	< 0.001***
	Residuals	272	0.41		
2010	Period	1	5.46	18.56	< 0.001***
	Impact	1	31.70	107.88	< 0.001***
	Period*Impact	1	1.26	4.29	0.039*
	Residuals	433	0.29		

Table 4. Results from ANOVA comparing sea cucumber density among periods (years before sea otter impact, years after sea otter impact), sea otter use (low use, moderate use, high use), and their interaction. P values, F statistics, degrees of freedoms (DF), and mean squares (MS) are reported. Significance levels are indicated with an (*), where * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

Source of Variation	*DF*	*MS*	*F*	*p*
Period	1	63.19	104.17	< 0.001***
Sea Otter Use	2	2.10	3.46	0.035*
Period: Sea Otter Use	2	8.50	14.01	< 0.001***
Residuals	118	0.61		

Table 5. Results from two-way repeated measures ANOVAs comparing sea cucumber density among area type (unfished area, neighboring fishing areas), year, and their interaction. Analyses were performed for two unfished areas with sea otters, 103-40 and 103-60, and two unfished areas without sea otters, 101-27 and 106-30. Only years with survey data in fished and unfished areas were used. P values, F statistics, degrees of freedom (DF), and mean squares (MS) are reported. Significance levels are indicated with an (*), where * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

Unfished Area	Source of Variation	*DF*	*MS*	*F*	*p*
103-40	Type	1	472.82	1.85	0.176
	Year	17	155.61	4.14	< 0.001***
	Type*Year	5	158.88	4.23	< 0.001***
	Residuals	491	37.58		
103-60	Type	1	5858.50	20.87	< 0.001***
	Year	17	166.75	4.22	< 0.001***
	Type*Year	6	40.83	1.03	0.402
	Residuals	410	39.48		
101-27	Type	1	0.58	0.00	0.983
	Year	19	414.91	3.10	< 0.001***
	Type*Year	12	215.44	1.61	0.084
	Residuals	568	133.77		
106-30	Type	1	100.40	0.03	0.867
	Year	15	682.09	2.66	0.001***
	Type*Year	8	297.42	1.16	0.321
	Residuals	423	256.05		

Figures

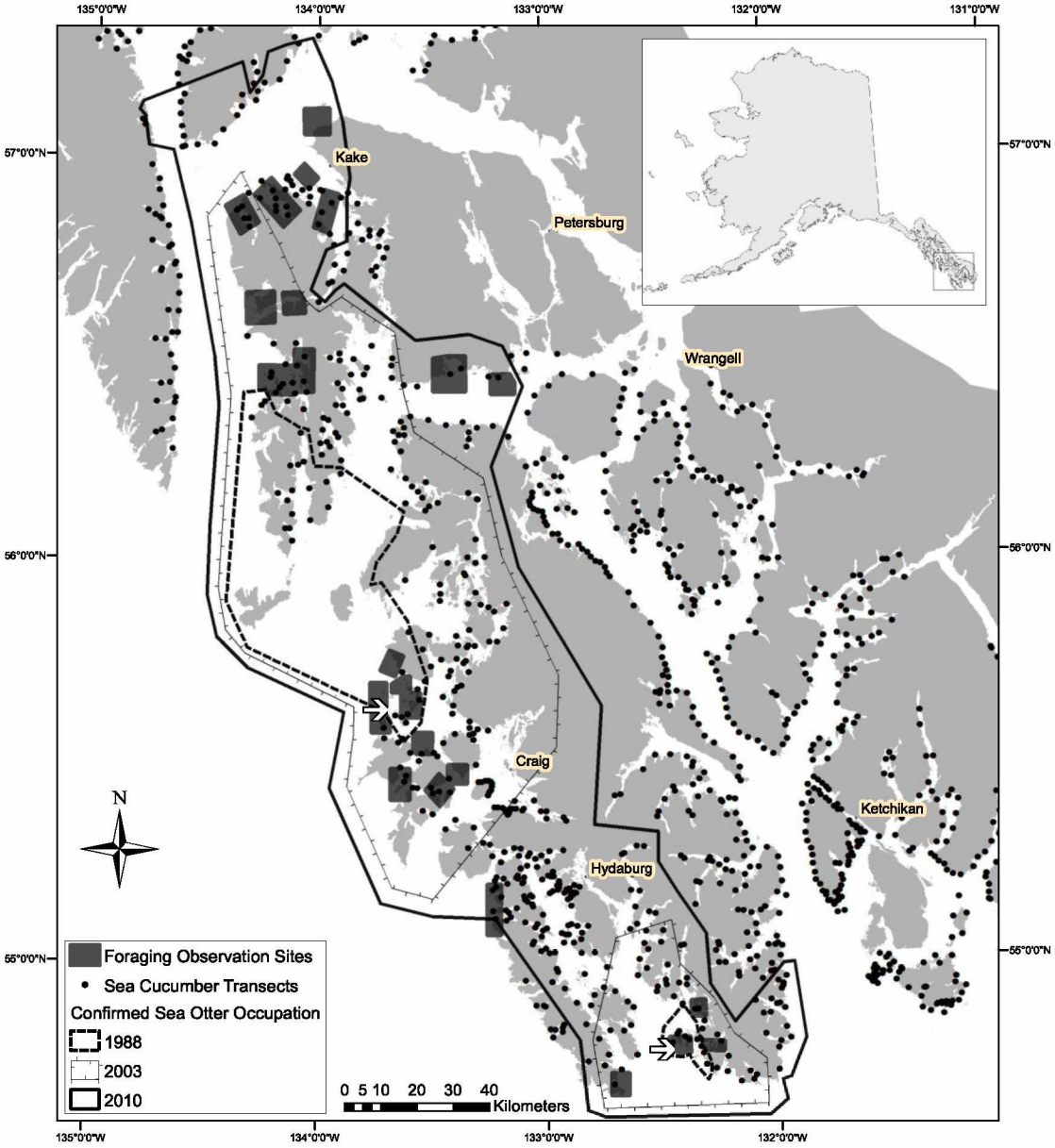

Figure 1. Southeast Alaska with estimated sea otter distributions in 1988, 2003, and 2010 and release sites (arrows). Sea cucumber transects (dots) represent sea cucumber density data and data collection sites (rectangles) represent sea otter foraging observations. (Pitcher 1989, Esslinger and Bodkin 2009, and V. Gill, USFWS Anchorage, AK, personal communication, 2012).

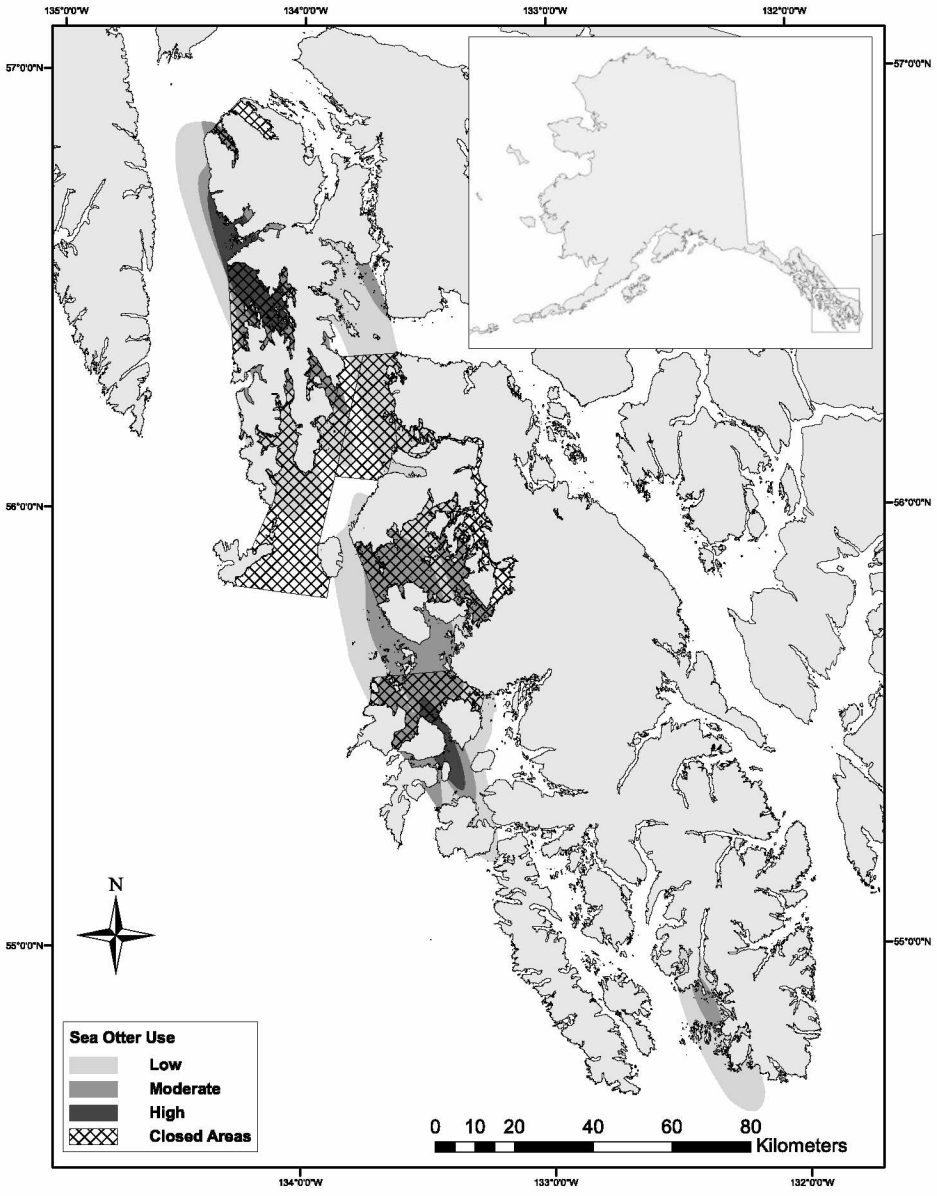

Figure 2. Southeast Alaska with fished areas that were closed due to low biomass (thatched polygons) (Rumble and Hebert 2011) and areas with low (light gray), moderate (darker gray), and high sea otter use (darkest gray). Sea otter use categories were derived from combined kernel density estimates for sea otter counts in 2003 and 2010 (Esslinger and Bodkin 2009, V. Gill, USFWS Anchorage, AK, unpublished data, 2012).

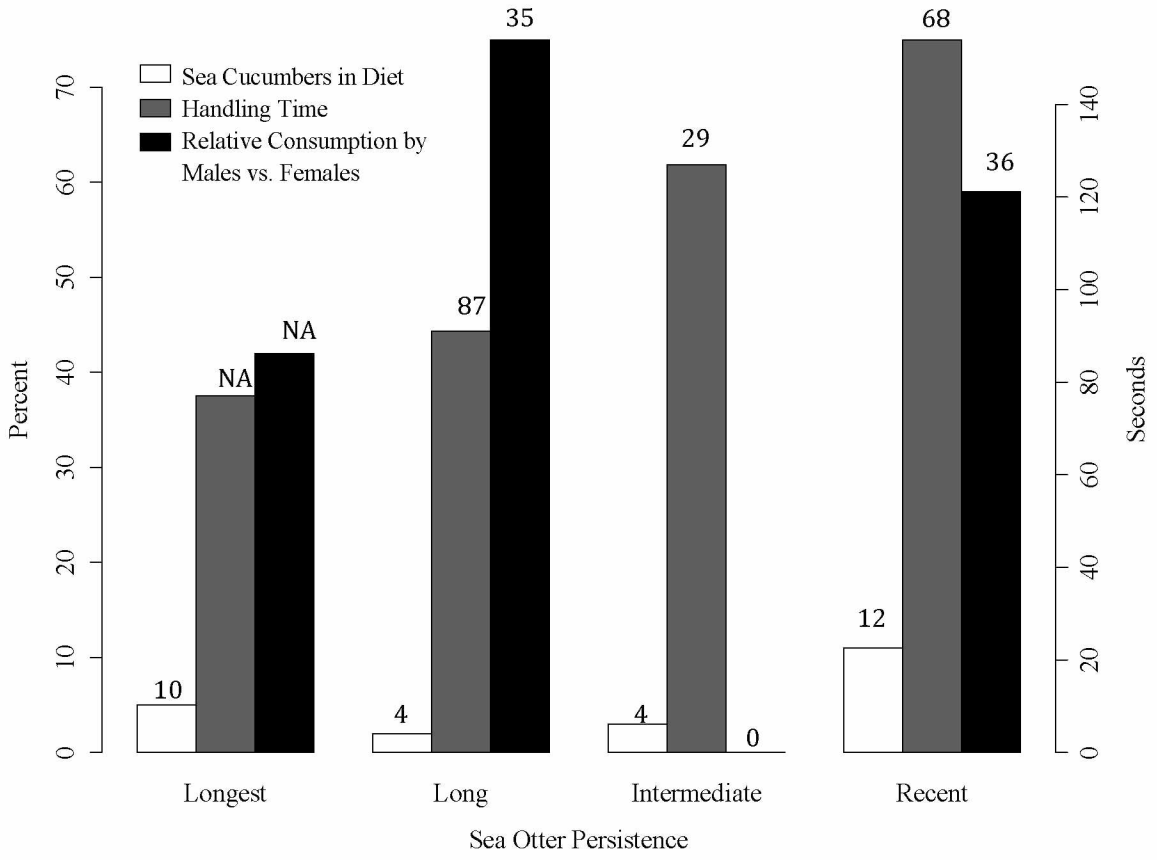

Figure 3. Mean percent sea otter diet, by edible biomass weight, consisting of sea cucumbers and relative sea cucumber consumption by males vs. females (primary axis) and mean sea cucumber handling times (secondary axis), at each sea otter persistence category. Standard deviations are located above the bars. Areas with longest, long, intermediate, and recent persistence had sea otters by 1988, 1994 or 1997, 2003, and 2010, respectively.

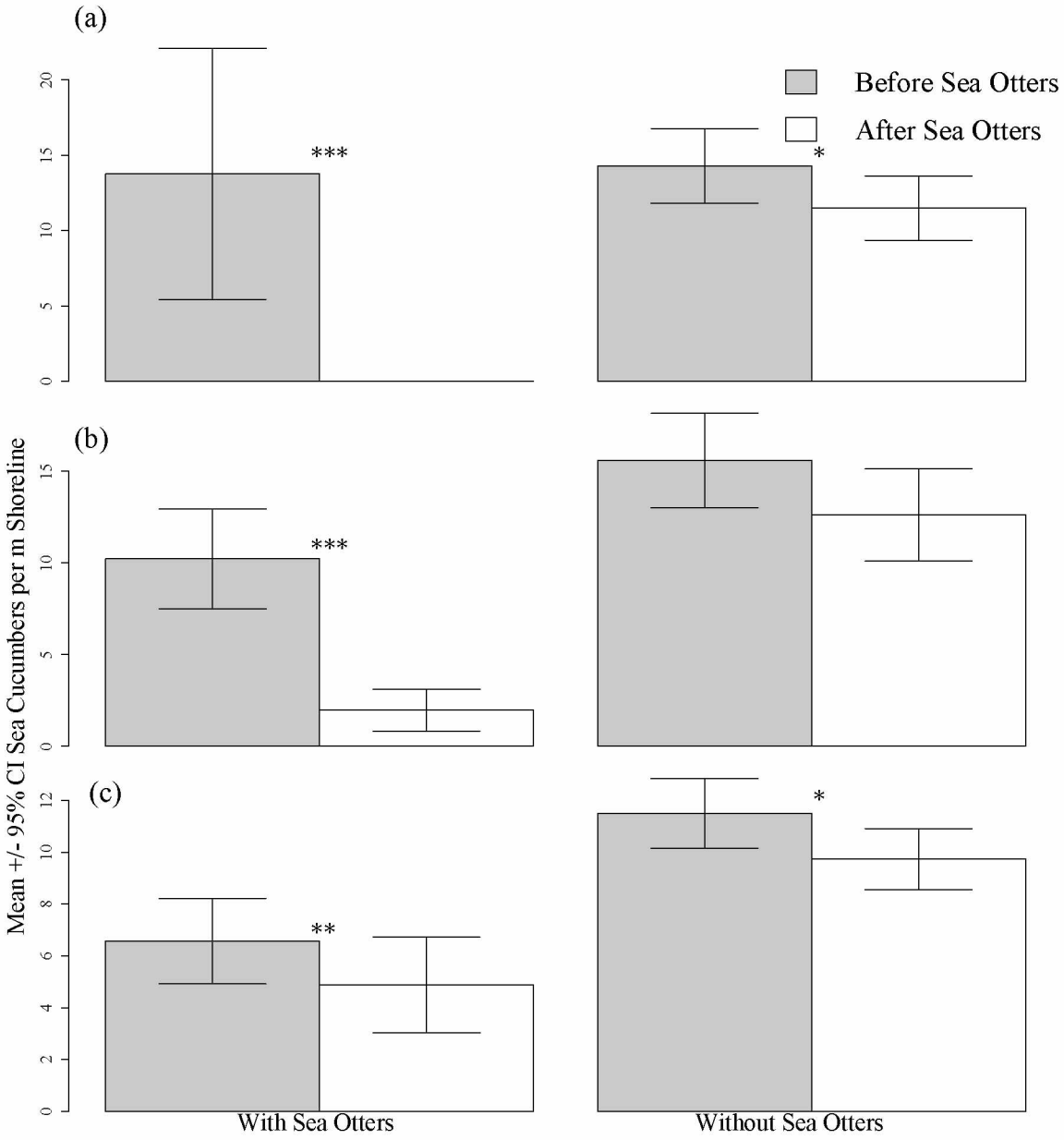

Figure 4. Mean sea cucumber density and 95% confidence intervals before (grey) and after (white) the presence of sea otters at affected transects with sea otters and control transects without sea otters. Comparisons were broken down to areas with a confirmed sea otter occupation in 1994 (a), 2003 (b), and 2010 (c). Significance levels from Tukey HSD pairwise comparisons between before and after periods are indicated with an (*), where * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

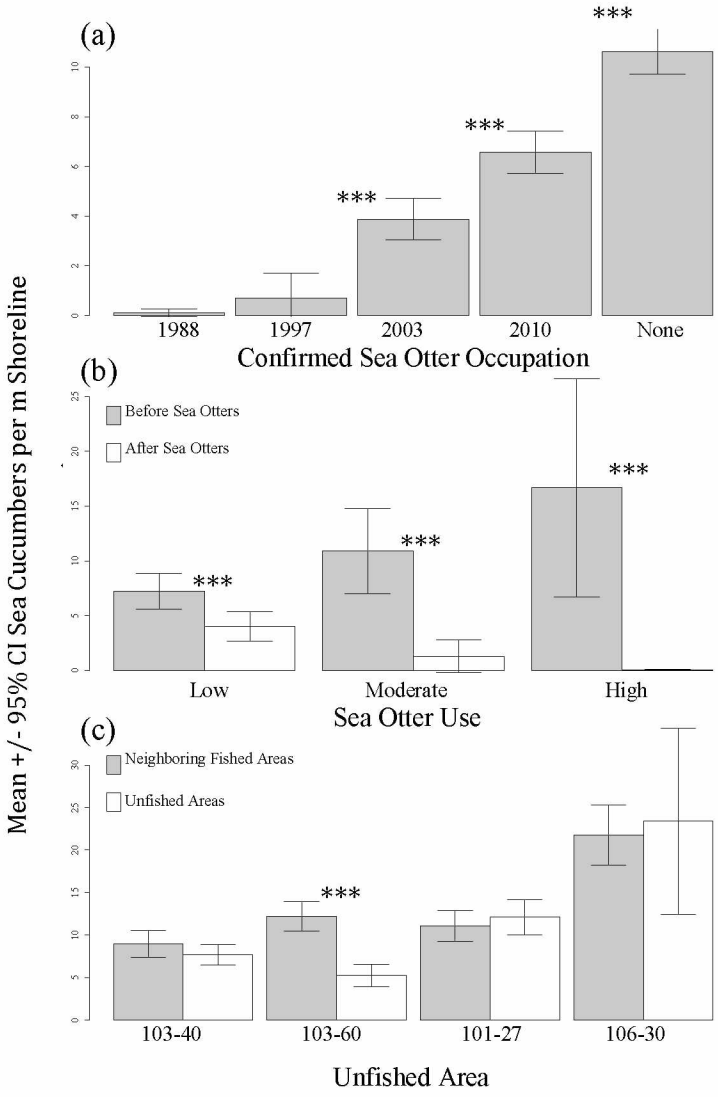

Figure 5. Mean sea cucumber density and 95% confidence intervals at (a) each sea otter category, including no persistence, (b) before (gray) and after (white) sea otter impact at each sea otter area use category, and (c) at the four unfished areas (white) and their neighboring fished areas (gray). Sea otters impact unfished areas 103-40 and 103-60. Density estimates in (a), (c), and the after period in (b) were based on ADF&G sea cucumber survey data from 2006 through 2011. Significance levels from Tukey HSD pairwise comparisons between before and after periods are indicated with an (*), where * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

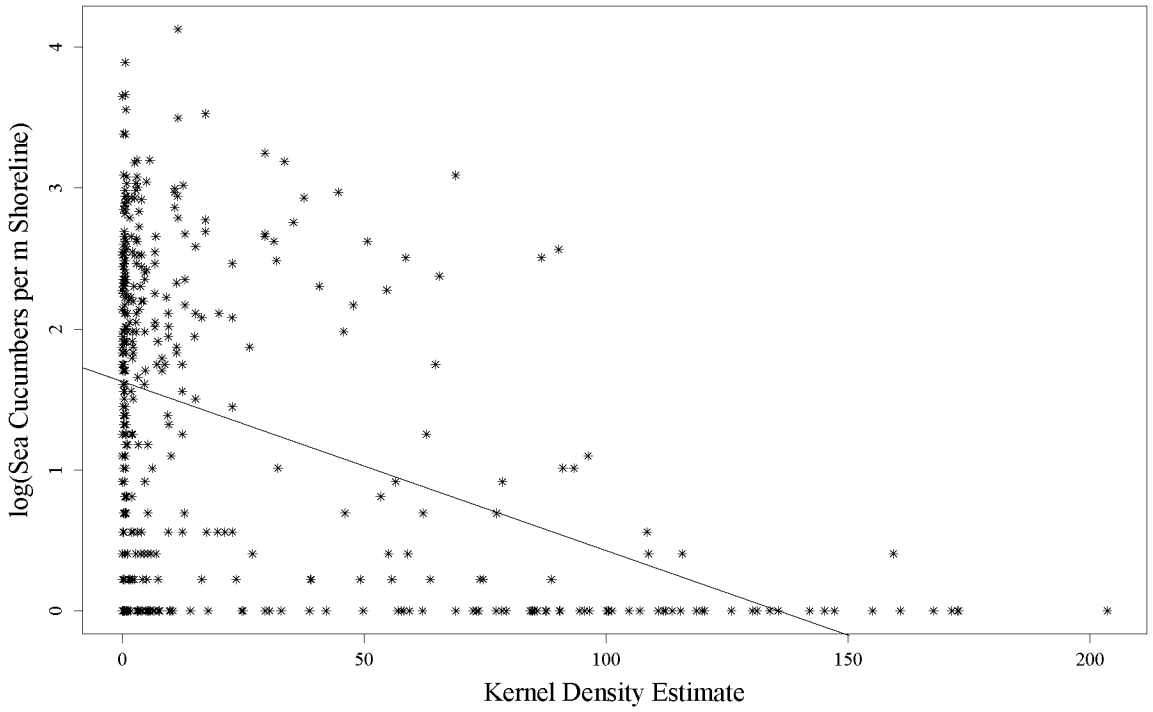

Figure 6. Log transformed sea cucumber density (sea cucumbers per m shoreline) versus combined kernel density estimates for sea otter distribution and abundance surveys in 2003 and 2010. The solid line is the fitted linear regression (r^2=0.23; F=17.50; df=419; $p < 0.001$).

General Conclusions

Reduced sea cucumber density from sea otter predation has direct implications to the sea cucumber fishery owing to management responses, such as area closures and reduced GHL. ADF&G surveyed Sea Otter Sound, located along west Prince of Wales Island, in 2011 and determined sea cucumber biomass was too low to allow a commercial harvest (Rumble and Hebert 2011). Sea Otter Sound was one of only two areas open to fishing that were within core sea otter ranges in 2010, and its closure marks the ninth fished area closed due to sea otter predation. Tebenkof Bay, located on the west sited of Kuiu Island, had sea otters by 1994 (Agler et al. 1995) and was closed to sea cucumber fishing in 1994 because of the "virtual elimination" of sea cucumbers (Rumble and Hebert 2011). ADF&G resurveyed Tebenkof Bay in 2011 and found that there had been no sea cucumber recovery and sea otters were still abundant in the area (Rumble and Hebert 2011). Nearly all fishery sub-districts that had sea otters by 1997 are closed to fishing because of low sea cucumber density. GHLs have historically remained relatively stable because of the addition of new fishery sub-districts, not corresponding to previously unfished areas used in this study. Between 2004 and 2011, 14 new fishery sub-districts were added to the fishery and two others were expanded; total initial GHL increase was 680,400 lbs (Davidson et al. 2008, Rumble and Hebert 2011). GHL in 2011 was reduced from 1,122,100 lbs in 2008 to 990,000 lbs (Rumble and Hebert 2011) and future reductions should be expected.

This study describes change in the sea cucumber resource and implies long-term

economic losses to sea cucumber fishermen in Southeast Alaska, but there are possible economic benefits to coastal communities and non-market benefits, i.e., existence value, to society as a whole. For example, sea otters can positively influence the economies of coastal communities by increasing opportunities for wildlife viewing and eco-tourism, i.e., revenue generated from local food vendors, shops and accommodations, or charter boat and kayak rentals. Estimates of the non-exploitative economic benefits of sea otters in California are in the millions of dollars (Loomis 2005). Sea otters also have existence value, i.e., the importance of their presence in an area is realized as one's "willingness to pay" (WTP). The per capita WTP of California citizens for the sea otter population in California was $27 in 2003 (Loomis 2005); however, given distinct social and cultural differences, it is inappropriate to assume that Alaskans look upon sea otters in the same light as Californians, and an economic assessment of net-economic benefits should be completed. This assessment should include economic losses to fishermen, processors and coastal communities, revenue generated from sea otter associated eco-tourism and recreation, and any indirect positive influences sea otters may have on other fisheries in Southeast Alaska. Kelp forests play a very important role in temperate marine ecosystems by providing habitat for, and stimulating the development of, kelp bed species (Estes and VanBlaricom 1985); therefore, sea otters have been hailed as necessary and critical for maintaining ecosystem health and function in these marine systems (Estes et al. 1989). Researchers are currently investigating how sea otters affect kelp forests and species composition at Vancouver Island, British Columbia; preliminary results suggest that kelp is deeper in the water column and encompasses more area, and

that some fish species are eating at higher trophic levels in areas with sea otters (Rebecca Martone, Institute for Resources, Environment and Sustainability, Vancouver, British Columbia, Canada, personal communication, 2012). Commercially important species that rely on kelp during any part of their life cycle may benefit from the proliferation of kelp forests that often accompanies sea otter recolonization. Pacific herring in Southeast Alaska support lucrative fisheries and deposit adhesive eggs onto a wide variety of substrates, including kelp (Scattergood et al. 1959). Productive kelp forests are found in areas of Southeast Alaska not yet impacted by sea otters and research is needed to identify how additional kelp benefits Pacific herring.

The proportion of the sea otter diets consisting of sea cucumbers was highly variable among study sites. This may be due to the relative abundance of other prey species and future research should include in situ surveys at foraging sites to test if sea otters are selecting sea cucumbers in proportion to availability. Seasonality may play a role in sea otter-sea cucumber dynamics, and future research should gather foraging data during multiple seasons: spring and summer when sea cucumbers are gravid and fall and winter during seasonal atrophy. In order to produce an accurate estimate of total annual sea cucumber removal, foraging data should be representative of the entire year, a task that is challenging financially and logistically.

Understanding the interaction between sea otters and sea cucumbers has value in terms of fisheries management, for providing some transparency into the sea otter conflict in

Southeast Alaska, and for conservation. Fisheries management predominately focuses on the optimal use of a species through single-species models without considering the role of ecosystem dynamics and regional processes (Levin 1999). Sea otter predation should be incorporated into management; i.e., areas with and without sea otters may need to be managed differently. Fishermen can use the results from this research to anticipate future changes to the fishery. Sea cucumbers also play a valuable role in a functioning ecosystem and are vulnerable to overexploitation (Conand 1990); therefore, their widespread removal may have significant effects on the nearshore marine community.

References

Agler, B.A., Kendall, S.J., Seiser, P.E., and Lindell, J.R. 1995. Estimates of marine bird and sea otter abundance in Southeast Alaska during summer 1994. U.S. Fish and Wildlife Service, Migratory Bird Management.

Conand, C. 1990. The fishery resources of Pacific Island countries. Part 2: Holothurians. FAO, Fisheries Technical Paper 272.2.

Davidson, B., Coonradt, E., Walker, S., Meredith, B., Breese, J., Harris, D., Thynes, T., Forbes, S., Pritchett, M., and Hoyt, Z. 2008. Annual management reports of the 2004/2005, the 2005/2006, and the 2006/ 2007 Southeast Alaska commercial fisheries for geoduck clams, red sea cucumbers, and red sea urchins. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Management Report 08–26.

Estes, J.A., Duggins, D.O., and Rathbun, G.B. 1989. The ecology of extinctions in kelp forest communities. Conserv. Biol. **3**:252–264.

Estes, J.A., and VanBlaricom, G.R. 1985. Sea-otters and shellfisheries. *In* Marine mammals and fisheries. *Edited by* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne. Allen and Unwin, London. pp. 187-235.

Levin, S.A. 1999. Towards a science of ecological management. Conserv. Ecol. **3**:6-9.

Loomis, J. 2005. Economic benefits of expanding California's Southern Sea Otter population. Report Prepared for Defenders of Wildlife.

Rumble, J., and Hebert, K. 2011. Report to the Board of Fisheries, Miscellaneous Dive Fisheries. Alaska Department of Fish and Game, Division of Commercial Fisheries, Fishery Management Report 11-59.

Scattergood, L.W., Sindermann, C.J., Skud, B.E. 1959. Spawning of North America herring. Trans. Am. Fish. Soc. **88**:164-168.